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Effects of mineral oil application on the orientation and feeding behaviour of *Macrosiphum euphorbiae* (Homoptera: Aphidae)

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Abstract: Application of mineral oil both in the fields and in the laboratory has been shown to efficiently reduce the transmission of non-persistent phytoviruses by aphids. In this study we investigated the influence a mineral oil spray on potato plants has on the behaviour of *Macrosiphum euphorbiae*, 24 h and 7 d after treatment. The aphid response towards oil treated plant volatiles was investigated using a darkened arena bioassay. The effect of oil treatment on aphid trophic behaviour was assessed using the electrical penetration graph (EPG) technique. Mineral oil treatment induced a lack of attractiveness of the host-plant, which lasted at least 24 h. The feeding behaviour of *M. euphorbiae* was modified on oil treated potato plants 24 h and 7 d after treatment. "Time from start of recording to first probe" was reduced but only significantly at 7 d after treatment, suggesting the facilitation of aphid stylet insertion. However, salivations phases and phloem sap feeding (ingestion phases) were significantly delayed. The modifications of aphid behaviour observed in this study are not drastic enough to explain the 7 d-protection observed in mineral oil sprayed fields and other potential mechanisms may exist.

Key words: *Macrosiphum euphorbiae*; mineral oil; electrical penetration graph (EPG); host-plant selection; olfaction

1 INTRODUCTION

Aphids are major pests for potato crops, essentially because they are vectors of numerous persistent and nonpersistent viruses. For instance, *Myzus persicae* Sulzer and *Macrosiphum euphorbiae* Thomas are polyphagous aphids able to transmit over 40 different species of viruses (Blackman and Eastop 1984). Spraying potato plants weekly with mineral oil has been shown to efficiently reduce nonpersistent virus transmission by aphids in both laboratory and field studies (Bradley *et al.*, 1962, 1966; Simons *et al.*, 1977; Vandervecken, 1977; Powell, 1992; Powell and Hardie, 1994). It has been suggested that mineral oil acts by inhibiting the binding or the release of virus particles in the aphid mouthparts or by delaying stylet penetration (Simons *et al.*, 1977; Harris, 1983; Powell, 1991). In 1992, Powell reported that mineral oil treatment on plants did not modify aphid superficial brief probes known to be responsible for virus acquisition and inoculation processes (Martin *et al.*, 1997). Mineral oil film on treated plant surface was suggested to disrupt virus retention in the aphid stylets (Wang and Pirone, 1996). However, the exact mechanism underlying this preventive effect is not yet completely understood. Researches have mainly focused on detailed interactions between aphid stylets and plant tissues just after mineral oil treatment on plants. However, weekly spray is necessary to give an efficient protection to crops. Thus, mineral oil spraying may induce other types of effects that may be delayed in time, before plant acceptance and stylet insertion, and/or more generally during aphid feeding and colonisation processes.

Potato plants constitutively release semiochemicals that play a major role in insect-plant interactions. It has been shown that aphids rely on chemical cues to locate and select their host plants (Pickett *et al.*, 1992; Powell *et al.*, 2006). Potato plant treatment with mineral oil may modify the chemical profile of the plant (either by masking the plant odour itself or adding a repellent effect) and subsequently affect insect-host plant location. This was indeed shown on sweet oranges where mineral oil sprayed leaves repelled citrus red mites *Panonymychus citri* (Cen *et al.*, 2002). Moreover, mite feeding, which involves gustatory cues, was also altered.

Therefore, modification of host-selection behaviour by mineral oil may be partly responsible for

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the inhibitory effect on virus transmission by aphids.

The objective of this study was to evaluate the influence of mineral oil spraying on potato plants (*Solanum tuberosum*) on the orientation and feeding behaviour of the potato aphid *Macrosiphum euphorbiae*. Potential effects of the oil treatment were also investigated in relation to time after application (24 h and 7 d).

2 MATERIALS AND METHODS

2.1 Plants and insects

Potato plants, *Solanum tuberosum* L. cv *Désirée*, were grown from tubers in 9 cm plastic pots in a growth room maintained at 20 ± 1℃ under a photoperiod of L16: D8. Four- to six-week-old plants were used for the experiments.

The *Macrosiphum euphorbiae* (Thomas) colony was initiated from a single apterous parthenogenetic female from the clone Me LB05 (INRA-INSA, Villeurbanne, France). Aphids were reared on potato plants (cv *Désirée*) raised under the same conditions in a separate growth room.

Two to three day-old apterous adult aphids were used in the experiments.

2.2 Mineral oil treatments on plants

Four-week-old plants were sprayed with the Finavestan EMA® (Total Fluides, Paris, France) mineral oil emulsified with water (3%, v/v). A hand-held trigger spray (Pulsar 1L, Tecnoma, Epernay, France) was used to evenly apply 6 mL of this emulsion to each plant, corresponding to the recommended dose for field application. The spray was applied from approximately 1 m above the plant to mimic field conditions treatment. Therefore only the axial surface of the potato leaves was sprayed. Treated plants were tested 24 h (OTP-1) and 7 d (OTP-7) after the spray. Untreated plants were used as control (CK). Indeed, preliminary experiments showed that aphids behaved in the same way (orientation and feeding behaviour) when tested on untreated plants or on plants sprayed with water 24 h or 7 d before the test (data not shown).

2.3 Effect of mineral oil treatment on plants on aphid orientation responses

The bioassay was realised in a darkened room maintained at 22 ± 1℃, and 35% ± 2% RH. The set-up (Ameline *et al.*, 2007) consisted of (1) an experimental arena made using a Plexiglas ® cylinder (14 cm diameter, 5 cm height) divided into 2 chambers and fitted with a floor made of a double polyethylene screen (mesh size approximately 0.5 mm). Two leaflets, belonging to 2 distinct whole plants, were inserted opposite each other *via* a 5 mm wide hole; (2) beneath the double screen, a 9 cm Petri dish containing 50 apterous aphids, previously starved for 2 h, was placed at the start of the experiment. In the dark, most aphids exhibit negative geotaxis and therefore climb on the mesh (Eigenbrode *et al.*, 2002). The double screen ensured that aphid mouthparts could not reach the leaflets. After 1 h of experiment, aphids positioned on either side of the mesh (corresponding to the 2 odour sources) were counted. Aphids located on the bottom of the Petri dish were considered as "non-responding".

To determine the influence of mineral oil treatment on potato plant on aphid orientation, a leaflet of a plant sprayed with oil emulsion either 1 d (OTP-1) or 7 d (OTP-7) before was assayed against an empty chamber referred to as blank (negative control) or against a leaflet of a control plant (CK) (positive control). To evaluate the sole effect of the mineral oil on aphid orientation, a filter paper (same size of a potato leaflet) sprayed 1 d before with the 3% oil emulsion (OTF-1) at the same dose than that used for the plant (*i. e.* 0.33 mL) was assayed against a blank. Eight replicates were made per treatment.

To avoid any possible bias, the device was rotated by 180℃ and the chamber was cleaned with TFD4 (Franklab S. A., Saint Quentin en Yvelines, France) between each replicate.

2.4 Effect of mineral oil treatment on plants on aphid probing behaviour

The Electrical Penetration Graph DC-system (Tjallingii, 1988) was used to investigate aphid probing behaviour on treated (OTP-1 and OTP-7) or control plants. To insert one aphid and one plant in an electrical circuit, a thin gold wire (20 μm diameter and 2 cm long) was stuck on the insect's dorsum by conductive silver glue, the other electrode was inserted in the soil of the potted plant. All plants and insects were held inside a Faraday cage during the 8 h recording at an ambient temperature of 20 ± 1℃. For each treatment, 20 – 28 replicates were done.

The acquisition and analysis of the EPG waveforms were done with PROBE 3.0 software (Tjallingii, Wageningen University, the Netherlands). Seventeen parameters belonging to five different EPG's waveforms (C, E1, E2, F and G) (Tjallingii, 1988) were calculated using the EPG-Calc 4.4 software (Giordanengo, 2008): C waveform corresponding to stylet pathways in plant tissues except phloem and xylem, E1 for salivation in phloem elements, E2 for passive phloem sap ingestion, G for active xylem sap ingestion and F for stylet desynchronisation (termed "stylet derailment").

The 17 EPG parameters were assigned to five categories (Table 1): (i) general probing behaviour class: this including the mean number of probes, the total duration of probing, and the time spent by aphids before initiation of the first probe; (ii) pathway phases that corresponded to searching activities performed by the aphids before reaching phloem elements; this class included the number of pathway phases and their total duration; (iii) salivation phases: including the number of probes before the first salivation phase (before aphids reached phloem elements), the time elapsed to the first salivation phase, the number of single salivations (occurring when a salivation period into phloem tubes was not followed by sap ingestion), and the total duration of single salivation phases; (iv) phloem ingestion phase (distinction was made between a phloem ingestion period shorter than 10 min and a sustained phloem ingestion period longer than 10 min, considered as a real ingestion phase): the phloem acceptance index corresponds to the percentage of time spent in feeding phloem sap after the first sustained phloem ingestion; (v) other EPG parameters were attributed to total durations of xylem ingestion and stylet derailment.

2.5 Statistical analysis

Statistical analyses were performed using STATISTICA 5.5 software (StatSoft, Tulsa, Oklahoma, USA). A Kruskall-Wallis ANOVA was performed to test the effect of plant treatment with mineral oil emulsion on insect orientation responses. Wilcoxon test for paired samples was used to analyse the distribution of responding aphids according to their position beneath the two chambers. EPG parameters of aphids feeding on treated (OTP-1 and OTP-7) plants were compared pair wise against the control plant (CK) with a Mann-Whitney *U* test at $P = 0.05$.

3 RESULTS

3.1 Aphid orientation responses

The percentage of non-responding insects was not significantly different between the experimental situations ($H = 2.05$; $P = 0.841$). Therefore we only considered the number of responding aphids for further analysis.

When tested against a blank, *M. euphorbiae* was significantly attracted by the control plant ($Z = 2.38$, $df = 1$, $P = 0.017$) (Fig. 1).

Aphids significantly preferred the control plant (CK) rather than a plant treated 24 h ago (OTP-1) ($Z = 2.10$, $df = 1$, $P = 0.035$) (Fig. 1). This suggests either a masking or a repulsive effect of OTP-1. However, aphids showed no preference for either a oil-sprayed plant (OTP-1) or a oil-sprayed filter paper (OTF-1) versus a blank ($Z = 0.42$, $df = 1$, $P = 0.674$ and $Z = 1.36$, $df = 1$, $P = 0.173$, respectively), showing that mineral oil was not repulsive but only masked the plant odour.

M. euphorbiae did not show any significant preference between the control plant (CK) and a plant treated 7 d before (OTP-7) ($Z = 0.56$, $df = 1$, $P = 0.575$). The latter was more attractive than a blank ($Z = 2.11$, $df = 1$, $P = 0.034$) (Fig. 1). This suggests that the mineral oil masking effect lasted more than 24 h but less than 7 d.

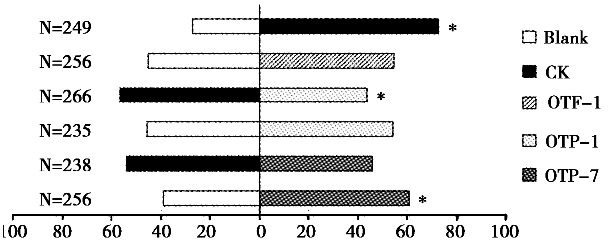

Fig. 1 Distribution of responding apterous *Macrosiphum euphorbiae* in the orientation bioassay

The bars represent the percentage of aphids positioned under each chamber; the number of responding aphids (N) is given on the left side of each experimental situation. Blank: Filter paper; CK: Control plant; OTF-1: Oil treated filter paper tested 24 h after treatment; OTP-1: Oil treated plant tested 24 h after treatment; OTP-7: Oil treated plant tested 7 d after treatment. Asterisks indicate a significant difference ($P < 0.05$) in the distribution of aphids between the two sides of the darkened arena.

3.2 Effect of mineral oil treatment on plants on aphids feeding behaviour

General probing behaviour (number of probes, total duration of probing, time to first probe) was not affected for aphids monitored on plants treated 1 d before (OTP-1) whereas on plants treated 7 d before (OTP-7), aphids showed significantly shortened time to the first probe ($U = 144$, $P < 0.001$).

Research activities performed by the aphids before reaching phloem elements (pathway phases) were also significantly modified only on OTP-7 plants by an increased number of pathway phases ($U = 231.5$, $P = 0.035$).

All the parameters in relation to salivation were significantly modified when aphids fed on OTP-1 plants (number of probes before first salivation: $U = 133$, $P = 0.008$; time to first salivation: $U = 1447.5$, $P = 0.019$; number of single salivation: $U = 122.5$, $P = 0.004$; and total duration of single salivation: $U =$

142.5, $P = 0.014$) while only the number of probes before a first salivation and the time elapsed to the first salivation were enhanced when aphids fed on OTP-7 plants ($U = 190.5$, $P = 0.005$ and $U = 237.5$, $P = 0.045$, respectively).

Some parameters regarding phloem ingestion were affected by the oil treatment. The number of probes before first phloem ingestion was significantly increased on both OTP-1 ($U = 156.5$, $P = 0.033$) and OTP-7 plants ($U = 200.5$, $P = 0.008$). Similarly, time to first sustained phloem ingestion was significantly enhanced whatever the time after plant spraying (OTP-1: $U = 164$, $P = 0.049$ and OTP-7: $U = 221$, $P = 0.021$). The phloem acceptance index of *M. euphorbiae* feeding on potato was significantly reduced 7 d after treatment ($U = 240$, $P = 0.050$).

Parameters linked to stylet derailment and xylem ingestion, respectively, were not significantly modified on treated plant.

Table 1 Probing behaviour of *Macrosiphum euphorbiae* during an 8 h access to leaflets of plants that are untreated (CK) or treated with mineral oil

	CK	OTP-1	OTP-7
EPG parameters	$n = 25$	$n = 20$	$n = 28$
General probing behaviour			
Number of probes	16.3 ±1.5	21.8 ±3.0	24.4 ±3.3
Total duration of probing (min)	335.7 ±30.1	304.5 ±21.3	347.5 ±25.0
Time from start of recording to first probe (min)	50.3 ±21.1	33.9 ±8.2	29.7 ±3.5*
Pathway phase			
Number of pathway phases	21.1 ±1.7	24.4 ±3.1	29.2 ±3.3*
Total duration of pathway phases (min)	147.1 ±22.7	153.0 ±16.1	195.6 ±18.3
Salivation phase			
Number of probes before a first salivation	6.9 ±1.2	13.1 ±2.2*	12.1 ±2.0 *
Time to first salivation phase (min)	110.7 ±32.1	223.8 ±34.2*	172.8 ±28.6*
Number of single salivation phases	2.1 ±0.3	1.1 ±0.2*	1.7 ±0.3
Total duration of single salivation phase (min)	5.5 ±1.6	2.2 ±0.7*	4.0 ±0.8
Phloem ingestion			
Number of probes before the first phloem ingestion	12.5 ±1.5	18.8 ±3.1*	20.6 ±3.1*
Time to first phloem ingestion (min)	154.9 ±35.6	275.0 ±32.8	210.2 ±32.2
Time to first sustained phloem ingestion (min)	231.5 ±33.2	334.9 ±36.5*	306.4 ±33.9*
Number of ingestion phases	1.4 ±0.2	1.2 ±0.5	1.6 ±0.4
Total duration of phloem ingestion (min)	135.2 ±24	80.7 ±26	89.7 ±22.5
Phloem acceptance index	35.5 ±6.0	25.3 ±7.0	24.2 ±5.9*
Other parameters			
Total duration of stylet derailment periods (min)	26.1 ±10.6	50.6 ±14.2	41.0 ±14.2
Total duration of xylem ingestion (min)	7.2 ±2.8	11.3 ±9.5	8.9 ±3.0

OTP-1: Oil treated plant tested 24 h after treatment; OTP-7: Oil treated plant tested 7 d after treatment. The data are the mean ± *SE*. Means followed by asterisk indicate a significant difference from control plants according to Mann-Whitney *U*-test at $P \leqslant 0.05$.

4 DISCUSSION

This study revealed that mineral oil treatment on potato plants could affect aphid orientation and trophic behaviour depending on the time elapsed after spraying.

Aphid orientation experiments showed that mineral oil treatment induced a lack of potato plant attractiveness, which lasted at least 24 h. Interestingly, the oil-sprayed filter paper did not induce any repellent effect on *M. euphorbiae*, as it is often the case with essential oils (Hori, 1998). Our results suggest that mineral oil treatment masked the attractiveness of the potato plant. It is the first time that such a behavioural modification triggered by a mineral oil treatment is reported in aphids.

The feeding behaviour of *M. euphorbiae* was altered on oil-sprayed potato plants 24 h and 7 d after treatment. Particularly, time to first probe was significantly reduced on plant treated 7 d earlier. This finding disagrees with a previous study which showed a delayed aphid stylet penetration on oil treated plants (Powell, 1992). However, this work was carried out with the aphid *Myzus persicae* on tobacco plants and the feeding behaviour was only recorded 24 h and 48 h after the oil treatment. Time to the first probe can be considered as the indicator of resistance factors located at the plant's surface. A long time to the first probe mainly reflects the effects of mechanical (*e. g.*, wax or toughness of the leaf surface) or chemical (*e. g.*, repellent volatile) stimuli present on the leaf surface (Alvarez *et al.*, 2006). Oil treatment acting as a wax solvent (McWhorter and Barrentine, 1988) may have partially removed it from the cuticle making epidermal tissues more accessible to the aphids. Our results seem to indicate that oil treatment facilitated aphid stylet insertion. However, this was not an immediate effect as "time from start of recording to first probe" was only significantly reduced 7 d after mineral oil treatment. Powell *et al.* (1999) also showed that *Aphis fabae* inserted its stylets more rapidly on oat cleaned of its epicuticular waxes.

The increased number of probes before the first salivation suggests that aphids had more difficulties in reaching the phloem tissues on treated plants. Whatever the time after plant treatment, the delayed phloem sustained ingestion, considered as the real ingestion phase, suggesting that aphids encounter difficulties in feeding. This is in accordance with the reduction of the phloem index after plant treatment. A long time elapsed before phloem access and sap ingestion can be considered as the indicator of mesophyll/phloem resistance factors. In addition, a low value of the phloem acceptance index has been related to a phloem-located resistance (Alvarez *et al.* 2006; Le Roux *et al.* 2008). Droplets of mineral oil have been reported to accumulate in the leaf intercellular spaces following spray application on citrus leaf (Tan *et al.*, 2005). Such accumulation of oil droplets within potato leaves may form oil plugs in the apoplasm thus disrupting stylet transit and enhancing the number of unsuccessful probes. The significant reduction of the phloem index value only 7 d after treatment suggests that oil droplets accumulation within plant tissues may have taken more than 24 h to occur. There is very little information about oil movement and persistence in plant tissues after spraying. Tan *et al.* (2005) suggested a potential movement and accumulation of mineral oil into various cells and tissues including phloem and xylem. Therefore, three hypotheses can be suggested to explain this general difficulty to achieve successful and stable phloem ingestion: (1) mechanical interference between the oil and the stylet (Powell and Hardie, 1994); (2) antiappetant properties of mineral oil leading the aphid to remove its stylets and feed for shorter periods of time; (3) indirect alteration of aphid behaviour *via* the plant response triggered following oil spray.

Our results show that aphids tested on oil treated plants exhibited a general higher probing activity and especially in epidermal tissues (higher duration and frequency of pathway phases). Powell (1992) showed that the occurrence of potential drops characterising brief probes in epidermal tissues was not modified after mineral oil treatment.

Under our experimental conditions, the modifications of aphid behaviour do not explain the 7d-protection observed in treated fields where mineral oil does not suppress but delays and reduces infections of aphid-borne non-persistently transmitted viruses (Webb and Linda 1993). Whereas these alterations of feeding behaviour do not invalidate the hypothesis of Wang and Pirone (1996) which supports that mineral oil interferes with the retention of virions in aphid stylets, they underline that oil spray induces secondary effects on plant-insect interaction possibly involved in oil preventive effect.

Further work is underway to investigate the way that mineral oil spray inhibits non-persistent virus epidemics.

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矿物油处理对马铃薯长管蚜定向和取食行为的影响

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摘要: 大田和实验室研究均表明矿物油的施用可有效降低蚜虫对非持久性病毒的传播。我们分别于矿物油喷施马铃薯植株24 h和7 d后,调查其对马铃薯长管蚜 *Macrosiphum euphorbiae* 行为的影响;采用暗室生测法调查了蚜虫对处理的植物挥发性化合物的反应;采用刺探电位技术(EPG)评价了矿物油处理对蚜虫取食行为的影响。结果表明:矿物油处理导致植物对寄主的引诱作用失效,这种效果至少持续24 h。矿物油处理马铃薯植株24 h和7 d后,蚜虫对处理植株的取食行为发生改变。开始记录至第1次刺探所需时间降低,但只在处理7 d后显著降低,提示矿物油处理有助于蚜虫口针的穿刺。然而,流涎阶段以及韧皮部汁液吸食阶段(摄食阶段)显著缩短。本研究中观察到的蚜虫行为的改变不能充分解释施用矿物油的大田中为什么出现7 d的保护作用,因此可能还存在其他的机制。

关键词: 马铃薯长管蚜; 矿物油; 刺探电位技术(EPG); 寄主植物选择; 嗅觉

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